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### Skeleton Bulk Biomass Ecosystem Model (SKEBUB)

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SKELETON BULK BIOMASS  
ECOSYSTEM MODEL (SKEBUB)

By

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## INTRODUCTION

Fisheries ecosystems have been modelled since at least the turn of the century. Nowadays the management of the world's fisheries is based, in part, on several well established models of varying complexity; for example, Schaeffer's surplus production model, Beverton and Holt's, or Ricker's, analytical models, and virtual population analysis. These models are based on a species by species approach to fisheries ecosystems, a fact which has led to criticism of their continued use, since the realization of the importance of species interactions.

To answer this criticism, models have been introduced which provide for interaction between the species in the management unit or ecosystem. This interaction has most commonly taken the form of interspecific predation and these models have undergone considerable development since their introduction to fisheries in the late 60's and early 70's. Ursin (1982) summarizes the models which have been applied to the management of marine fisheries.

A consequence of the increased complexity of these models over the single species approaches has been the requirement for more and more data and, when these data are not available, their estimation or substitution with unproven formulae. This has led to a reluctance to incorporate multispecies models into fishery management decisions and occasionally their derision in the scientific press (Gulland 1982). A diversity of available models has resulted, from the concise multispecies virtual population analysis (e.g. Pope 1979) with biologically identifiable data requirements, to the detailed analytical model of Anderson and Ursin (1977) with requirements for parameters of ambiguous biological meaning. Both approaches have their merits and it is only through the continued development of models and their comparison that a holistic view of fisheries ecosystems will be obtained.



A model lying between the two extremes in complexity is presented here. It is a simplification of the extensive biomass-based models of Laevastu and Larkins (1981) without spatial resolution. The formulae used in this model correspond to those of the larger models (DYNUMES and PROBUB) and are characterized by their straightforward relationship to the available data. Unknown parameters and coefficients for which there are little or no data are kept to a minimum. In general, the formulae are of a linear form, in the absence of any biologic information to the contrary.

Abbreviated ecosystem models are an aid in evaluating the relative importance of component processes in the ecosystem. They have the advantage of being readily assimilable by both the modellers and their audience, but they are a simplification. Lack of spatial heterogeneity and a lack of recruit variability in particular, limit the results to average solutions. Their purpose is not to attempt to define the ecosystem and its processes, but rather to foster an understanding of the general interactive processes.

This paper presents the formulae used in the model, followed by a more detailed examination of the interactive processes in the feeding routines. The reader is referred to Laevastu and Larkins (1981) for a comprehensive discussion of the attributes of biomass-based models in general. It is stressed that the formulae presented herein are not invariable, but should be changed to reflect available information on the species under consideration or the beliefs or hypotheses of the researcher. Sample input data and parameters are presented in the following sections, together with results from this preliminary modelling. The species composition has a rough correspondence with that of Georges Bank, but the data do not necessarily correspond to published data.



## FORMULAE IN SKEBUB

### Monthly Changes in Biomass

#### APEX PREDATORS

The apex predators are divided into three groups--mammals, birds, and sharks. Because of the high mobility of these predators, their biomasses are not computed in this model. The mean annual biomass of each predator group is an input value. Monthly deviations from this mean biomass are described by a simple harmonic formula, (cosine), where the frequency and magnitude of the oscillations are input values, and can be used to describe migrations in and out of the area.

#### FISH SPECIES AND BENTHOS

The following set of equations applies to benthos and all groups of fish species with the exception of the squids. The data on the squids are insufficient to enable the dynamic computation of their biomass, consequently, their biomass is maintained in the same manner as the apex predators. Other species do prey on the squids and the squids do prey on other species.

The central formula for the monthly updating of biomass of a species grouping (N) in month k is:

$$BB_{N,k} = BB_{N,k-1} * e^{GS_{N,k} - GMS_{N,k} - FP_{N,k} - C_{N,k}}$$

where  $GS_{N,k}$  is the growth,  $GMS_{N,k}$  the natural mortality excluding predation,  $FP_{N,k}$  the fishing mortality, and  $C_{N,k}$  the consumption of N by other species. An iterative procedure is used to update this equation:

a) an initial, and approximate, computation uses the previous month's (k-1) values of growth, natural mortality, fishing mortality, and predation. This





computation is used to determine the current month's feeding computations.

b) the computation is repeated with the component parameters adjusted to reflect the current month's feeding and biomasses, as indicated below.

c) step b is repeated until the biomasses values of successive iterations converge. In practice it has been found that the values converge rapidly and step b is computed once only.

#### ZOOPLANKTON AND PHYTOPLANKTON

The monthly biomasses of zooplankton and phytoplankton are computed in the same manner as those of the apex predators, namely, an input mean annual biomass is adjusted by a cosine function to simulate seasonal variation. The period and magnitude of this seasonal variation are controlled by input parameters.

#### Components of the Biomass Equation

All components of the biomass equation are adjusted monthly by any or all of: temperature, starvation and, following equilibrium, density dependent factors.

#### GROWTH ( $GS_{N,k}$ )

Species specific input values for growth ( $G_N$ ) are adjusted in the following equations. The last of these equations (density dependence) is only computed once equilibrium has been reached.

$$a) \quad GS_{N,k} = G_N * e^{\left(\frac{1}{TA} - \frac{1}{TM}\right)}$$

Growth is adjusted by the difference between the current month's temperature,  $TM$ , and the optimum, or acclimatization, temperature for the species,  $TA$ . Both values are input parameters. The form of the equation follows Krueger (1964).

$$b) \quad GS_{N,k} = GS_{N,k} - (SC_N * 0.01 * GS_{N,k})$$



The growth rate of any species is reduced by the fraction of its food requirement that it could not obtain in the current month, ( $SC_N * 0.01$ , where  $SC_N$  is a percentage). This adjustment is thus dependent on the biomass of the species itself (i.e., its food requirement), and the biomass of the other species which provide, or remove, potential prey items. This effect is assumed to be linear, following Jones and Hislop (1978).

$$c) \quad GS_{N,k} = GS_{N,k} + \log_e \left[ \frac{V_N}{\overline{BB}_{N,1} * 12} \right]$$

To provide for density dependent growth once the equilibrium position has been reached, the growth for each species is adjusted by the ratio of the equilibrium biomass of that species ( $V_N$ ) to its mean biomass in the previous year, ( $\overline{BB}_{N,1}$ ). This ratio is divided by 12 to correspond to the monthly growth coefficient. The natural logarithm of this ratio is taken to correspond with growth, which is expressed as an instantaneous rate.

Density dependent growth has not been identified as a universal characteristic of fish species and potential researchers will have to consider the suitability of this equation in their own situations. Implicit in the use of this equation in this instance is the assumption that decreases in the biomass are linked with reduction in the percentage of adults in the population (e.g., resulting from fishing mortality). Individual growth rates decrease with increasing age (Paloheimo and Dickie 1965) thus the decrease in mean age of the population will produce an increase in mean biomass growth rate.

#### NATURAL MORTALITY ( $GMS_{N,k}$ )

Natural mortality excludes that due to predation, which is computed separately. It includes spawning stress and senescent mortality, together with residual



mortalities, for example, mortality due to disease (Laevastu and Larkins 1981).

Input, species specific, natural mortality ( $SM_N$ ) is assumed to increase as a linear function of starvation ( $SC_N$ ):

$$GMS_{N,k} = SM_N + (SM_N * SC_N * 0.01)$$

#### FISHING MORTALITY ( $FP_{N,k}$ )

The fishing mortality has two components--a constant rate of mortality,  $FK_N$ , and a density dependent component,  $FM_N$ . Before equilibrium, total fishing mortality is simply set at twice the constant component (i.e.  $2 \times FK_N$ ). This value corresponds to the available data on fishing mortality. After equilibrium, total fishing mortality is equal to the constant rate plus the density dependent component. The form of this density dependence is currently represented by the following equation:

$$FM_N = FK_N * \sqrt{\frac{BB_{N,0}}{V_N}}$$

$$FP_N = FM_N + FK_N$$

The division of the fishing mortality into two components allows the consideration of the relatively constant components (e.g., bycatch and artisanal fisheries) separately from the density dependent component (e.g., management adjustments). This formula may be modified in future simulations to incorporate species specific factors.

#### CONSUMPTION BY APEX PREDATORS (SS)

The food requirements of the apex predators are a function of their biomasses. Monthly variations in the biomass, and therefore the food requirements, do occur, but from year to year they are invariant. Consequently, their food requirements are computed once at the beginning of the model. Together with the percentage



food composition table for each predator, this gives the monthly consumption of each prey group by the apex predators. This is removed each month irrespective of the current biomass of any of the prey groups. In areas with high apex predator biomasses this would need adjusting to allow prey switching in response to prey availability.

#### CONSUMPTION BY OTHER SPECIES ( $CC_{N,k}$ )

Food requirements of these species groupings are dependent on their growth in the current month. Initial estimates of growth in any month are computed using the previous month's values for the parameters in the biomass equation. Once consumption is computed, the growth is recomputed. It is possible to recompute consumption at this stage to reflect the updated growth, but in practice this has not been found to affect the results. Thus the consumption is computed only once in each month. The steps are as follows:

#### Total Food Requirement of Each Species Grouping ( $FOOD_N$ )

The food requirement consists of a food requirement for growth and a food requirement for maintenance. The food requirement for growth is computed from the actual growth in biomass, ( $GRO$ ), that is, growth uncorrected by fishing mortality, natural mortality, or consumption:

$$GRO = BBI * (e^{GS_{N,k}} - 1)$$

The maintenance requirement is computed as the maintenance requirement for the mean of the current and the previous month's biomass,  $BBI$ . An arithmetic mean is used following Ricker (1975, p. 239). Thus the total food requirement can be expressed as:

$$FOOD_N = (BBI * FRM * 30) + (GRO * FRG)$$





where FRM is the coefficient for daily food requirement for maintenance, and FRG is the coefficient of food requirement for growth. Both coefficients are expressed as a fraction of the biomass or growth in biomass, and are input parameters.

Amount Consumed of Each Prey by Each Predator ( $CPN_{N,k}$ )

There are two sets of inputs that determine the amount of consumption of a prey group by a predator. Firstly, a table of the percentage food composition of each predator (derived from stomach analyses modified to include the juvenile feeding) is input,  $CF_{N,k}$ , and together with the food requirement for each predator, ( $FOOD_N$ ), the actual food required by each predator group from each prey group, ( $CPN_{N,k}$ ), is determined. These values are summed over each prey group to give the total amount of food required from each group, ( $CC_{N,k}$ ).

Total food requirement ( $CC_{N,k}$ ) is compared with the allowable consumption of each prey group's biomass, ( $AC_k$ ). The allowable consumption is the second set of input values, where the allowable consumption is input as a percentage of that prey group's biomass, ( $AP_k$ ), and the allowable consumption, ( $AC_k$ ), is computed from the current biomass of that group.

At this stage, then, the food required by each predator group of each prey group and the allowable consumption for each prey group are known. These values are now used to modify the input food composition table to reflect the influence of prey abundance on feeding. The ratio of allowable to required food consumption of each prey group is formed, ( $FCOC_k$ ), and the adjusted percentage food composition of the predator's diet is made a function of this ratio and the input percentage food composition:

$$FCN_{N,k} = CF_{N,k} * \frac{1 + Ae^{-B}}{1 + Ae^{-B*FCOC_k}}$$



where A and B are input parameters which determine the magnitude and rate of any change in food composition, respectively. The effect of this equation is described in more detail in a later section. The modified food composition table, (FCN), is now used to recompute the actual food requirement of each predator from each prey group, which is again compared to the amount allowable from that prey group, and if overconsumption of any prey group is still indicated, the excess is removed from the predator's food for that month. The difference between the required and the actual food consumption for any group is then allotted to starvation, ( $SC_N$ ).

#### Calculation of Equilibrium Biomasses

Equilibrium is attained when the biomasses of the species groups are constant from one year to the next. Monthly fluctuations do occur due to seasonal variation in temperatures, apex predator consumption, and phytoplankton and zooplankton biomasses. At equilibrium the growth in biomass must equal the losses to each biomass from fishing, predation, and natural mortality. Thus, to attain equilibrium, either the growth of the species can be varied, or the sources of loss can be varied, but in an opposite direction. Growth is determined from empirical data, and the mortality coefficients for fishing and natural causes are assumed to remain constant from year to year (before equilibrium). Predation is the logical variable to adjust to reach equilibrium and, rather than adjust the percentage food composition (derived from stomach samples), the input biomasses of the species groups are modified. An iterative procedure is used which adjusts the biomasses at the end of each year's computations:

$$BB_{N,12,b} = BB_{N,1,a} + \frac{BB_{N,12,a} - BB_{N,1,a}}{AGA}$$



where  $BB_{N,12,b}$  is the new December biomass,  $BB_{N,1,a}$  is the previous year's January biomass, and  $BB_{N,12,a}$  is the current December biomass. The iteration constant, AGA, controls the degree of convergence towards the equilibrium and varies from 3.0 at the beginning of the iterative procedure to 4.8 at the end of the iterative procedure. Thirty iterations, or "years", have been found necessary to reach a stable position.<sup>1/</sup>

#### SIMULATION OF FOOD SUITABILITY AND AVAILABILITY DEPENDENT FEEDING

Predator-prey relationships provide a readily comprehensible mechanism for species interactions and are used for this purpose in many ecosystem models (e.g., Andersen and Ursin 1977, Pope 1979, Helgason and Gislason 1979, Laevastu and Larkins 1981). Ursin (1981) has discussed the constraints of the models of Pope(1979) and Helgason and Gislason (1979), in particular their assumption that growth and food consumption rates are independent of food concentration. The remaining two models allow underconsumption by a predator species when prey sources are limiting. In both instances the prey consumption by a predator is made dependent on an index of suitability and the prey's biomass.

Andersen and Ursin (1977) compute the suitability, or vulnerability, index as a composite of suitability with respect to size, the fractional overlap of predator and prey in time and space, and the chance of encounter due to the behavior of predator and prey. This index is frequently compared with available stomach contents data to check the realism of the arrays. Laevastu and Larkins (1981) have taken a more direct approach and base their suitability index on

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<sup>1/</sup> A "stable position" is defined as one where further iterations do not affect year and biomasses. In practice this stabilization occurs when the percent annual change in individual biomass varies from 0 to about 5%. Global adjustment to the allowable percent consumption parameter is used to adjust the equilibrium position so that the mean of the percent annual changes in individual biomasses (which can be + or -) is close to zero.



empirical data from stomach content analyses.

The proportion of a prey actually "occurring" in a predator's diet in each time step is then made a function of this suitability index and the prey's current biomass. In the Andersen and Ursin (1977) model, prey switching by a predator is implicit and is in direct proportion to the relative proportion of each prey biomass. Laevastu and Larkins (1981) explicitly allow prey switching; the suitability of any prey type at any time step is a function of the input suitability index and the ratio of required to available biomass for each species. This latter approach requires the input of a parameter to determine the proportion of each biomass available for consumption in each time step; otherwise overgrazing would occur. This parameter is a fixed proportion of the growth for all fish species. In the model of Andersen and Ursin (1977), actual food consumption by any predator is then determined from the available prey and a half saturation constant, or coefficient of rate of search. Once the adjusted suitability index has been computed in the Laevastu and Larkins (1981) model, no further adjustment to feeding occurs; if more food is required from a prey biomass than is deemed allowable, the predators requiring that food suffer starvation. Both models, then, require the estimation of a parameter unverifiable given current data. The method of Andersen and Ursin (1977) computes the half saturation constant for each species by trial in the model. Laevastu and Larkins (1981) designate allowable consumption as a fixed proportion of growth for all species. In SKEBUB this proportion is assumed identical for all fish species, reducing the required parameter estimates to one. This global allowable consumption parameter is adjusted so that the estimates of the percent of required food that is unobtained (starvation) appear consistent with available data. The method of Laevastu and Larkins (1981) as used





in SKEBUB is presented in more detail below. The function relating the composition of the diet to the biomass of the prey is modified to allow the modeller to control the dependence of the final food composition of each predator on either the input table of selectivities or on the allowable composition of each species.

#### SIMULATIONS OF FEEDING IN SKEBUB

At the beginning of each monthly time step the growth of each biomass and the food required for the maintenance and growth of this biomass are computed. The food required by each predator of each prey is then determined through the input food selectivity table ( $CF_{N,k}$ ). The total requirement for all predators from each prey type is computed and compared with the amount of each prey biomass designated available. The input food selectivity table is now adjusted by a function of the ratio of available to required food for each prey biomass, ( $FCOC_k$ ):

$$FC_{N,k} = CF_{N,k} [(1 + Ae^{-B}) / (1 + Ae^{-B(FCOC_k)})]$$

where  $FC_{N,k}$  is the adjusted percentage food composition, and A and B are constants.

This equation is a modification of the logistic equation, forcing the point of inflection to be at  $x = y = 1$  (i.e. when the food required from a prey type is equal to the amount available, ( $FCOC_k = 1$ ), no adjustment is made ( $FC_{N,k} = CF_{N,k}$ )). The maximum upward adjustment of the percentage food requirement from any prey item is equal to:

$$MaxUp = 1 + Ae^{-B},$$

and the maximum downward adjustment:

$$MaxDown = MaxUp / 1 + A$$

The rate of change is specified by B, although a value of 1.5 has been found reasonable in practice. The effect of increasing A is a parallel increase in the maximum upward and downward adjustments.



## Results and Limitations

Complete utilization of all available prey can be obtained with a high value for A or by iterating the procedure several times. Five iterations with  $A = 1.5$  and  $B = 1.5$  produced complete consumption of all prey biomasses when prey was limiting. Although, superficially, this appears reasonable, it is apparent that the feeding routine becomes highly dependent on the amount of each biomass designated available for consumption which is difficult, if not impossible, to quantify. In practice, one iteration with  $B = 1.5$  and  $A = 1.5$  was found satisfactory, producing a stable equilibrium position with the equilibrium food composition reflecting the input distribution.

The approach is versatile enough to enable emphasis to be put on either the input food composition table, or on the estimated prey availability. The level of adjustment can be made specific to each predator biomass and used to investigate the effects of a high or low prey selectivity by a predator.

## PRELIMINARY RESULTS FROM SKEBUB

These results illustrate the output from a simulation on the sample data given in Appendix Tables 1 to 6. They are presented here to provide the reader with an illustration of the simulations in SKEBUB and are not intended to test biological hypotheses.

Many data result from a single run of SKEBUB. Laevastu and Bax (1982) detail possible data outputs. Here we present mainly annual mean biomasses of the various species groupings. There are two stages in the simulation. The first stage produces an equilibrium situation given the input data. The equilibrium biomass of a species group is that biomass which can be sustained such that the growth of the biomass equals its mortalities. The equilibrium situation may be considered an unnatural one, but it is a necessary starting



point and base for the comparison of the effects of various factors on the ecosystem (Laevastu and Larkins 1981). Figure 1 illustrates the changes in the species groups biomasses from their input until equilibrium is reached 30 years after the start of the run. The biomasses change again immediately following equilibrium when the equilibration procedure is removed and the input food selectivity table is replaced by the one adjusted at equilibrium. This replacement of the input food composition table is not necessary to the running of the model and is inadvisable when the input food composition table is estimated with confidence.

After equilibrium the density dependent influences on growth come into play and maintain the biomasses at a fairly constant level (years 1 to 9, Fig. 2). In the tenth year following equilibrium two severe and arbitrary adjustments were made to the biomasses to study the maintaining effect of the density dependent processes. In Figure 2 the biomass of the silver hake species group was reduced by 75 percent at the start of year ten. In the subsequent ten years all biomasses fluctuate until approximately the original equilibrium distribution of biomasses is regained. In Figure 3 the fishing pressure on the silver hake species group was raised fourfold at the start of the tenth year following equilibrium. Again equilibrium was regained in the subsequent ten years, but in this instance a new equilibrium distribution of biomasses was reached, reflecting the continuing effect of the increased fishing pressure.<sup>2/</sup>

Sample output data are given in Table 1. These data are the annual mean values at equilibrium.

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<sup>2/</sup> The ordinate scale varies for each species group on these graphs. The biomass of benthos was reduced by a factor of 10 for plotting.



SKEBUB can thus be run in two modes. In the first instance, input variables are modified and the output data at equilibrium compared. This provides information on the sensitivity of the simulation to changes (or error) in the input data and demonstrates the interactive effects of the model. This mode is used to investigate the relative importance of parameters or species groups to the overall biomass and to the biomasses of other species groups. The second mode starts when the equilibrium forcing constraints are replaced with density dependence and is primarily of use in studying the interactions of the species groups following a perturbation (e.g. increased fishing effort on one species). The time scale of these interactions is strongly dependent on the form of the density dependent formulae.

As is the case with all simplified ecosystem models it is the repeated running and hypothesis testing that provides the most information, rather than the actual output data from any one simulation. For this reason the code of the model has been kept simple to facilitate users in developing a clear understanding of the component processes. Processing time for a 70 year simulation with 13 species groups is under 30 secs. on a Burroughs B7800 mainframe computer, and has a core requirement of less than 8000 words. The FORTRAN code for SKEBUB is available as printed output or on 5 1/4 inch soft-sectored diskettes written on an Osborne 1 micro-computer,





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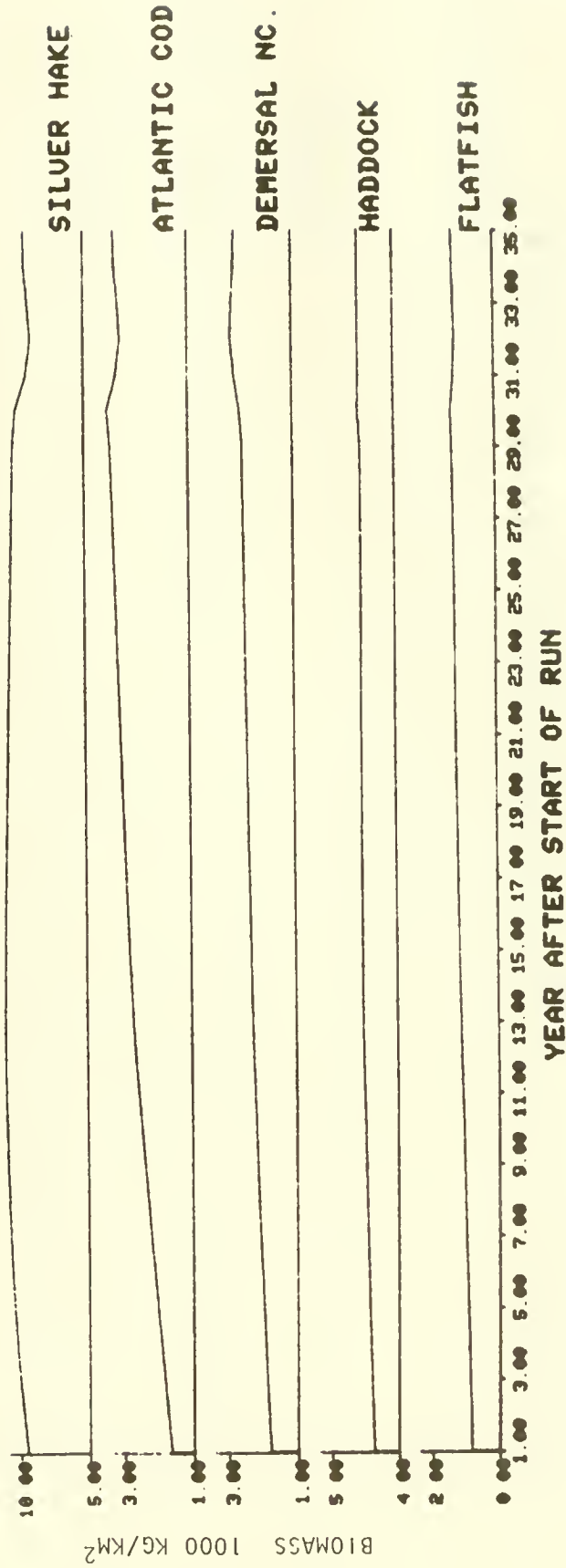


Figure 1. Annual mean biomasses of fish species groups and benthos, showing the change from input to equilibrium values.



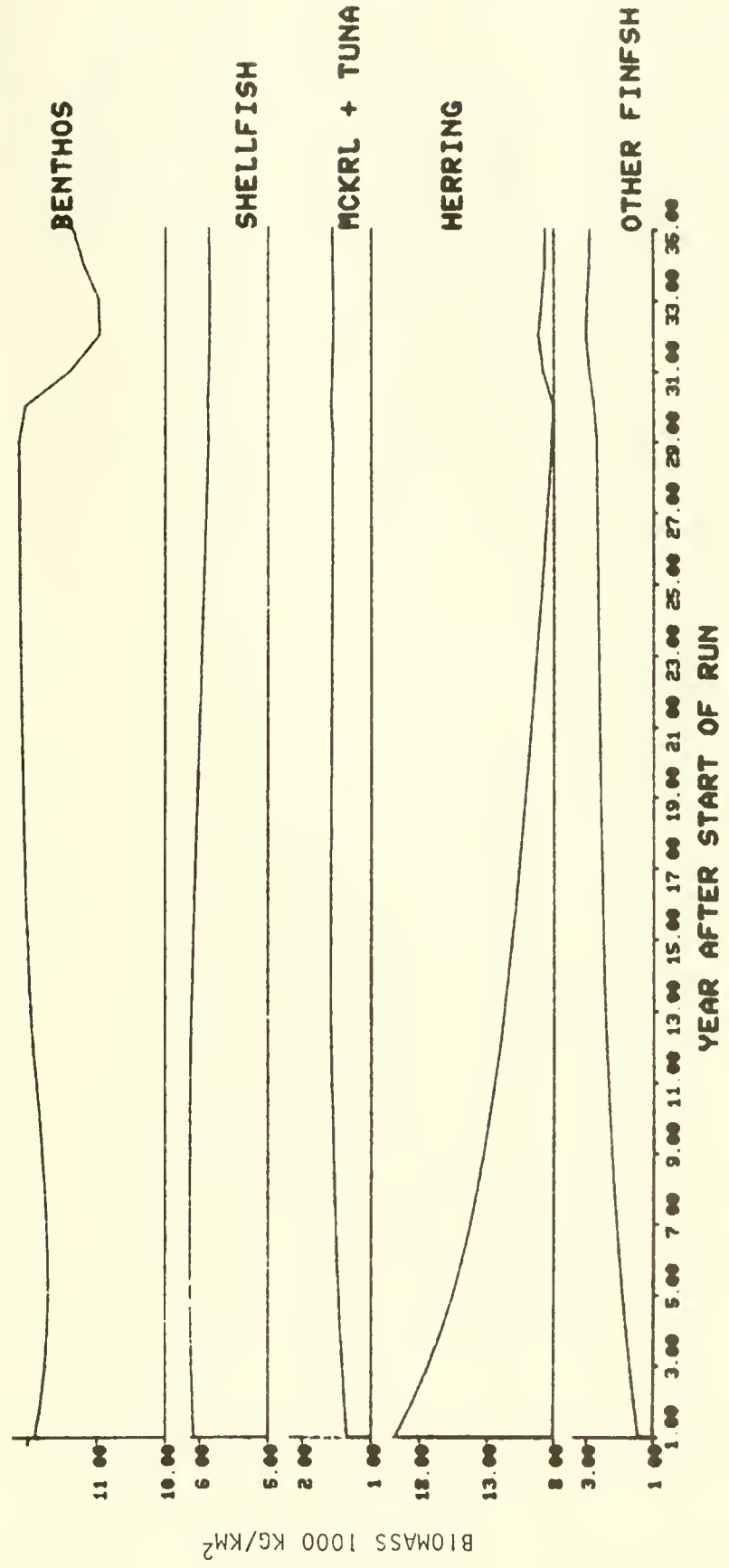


Figure 1. cont.





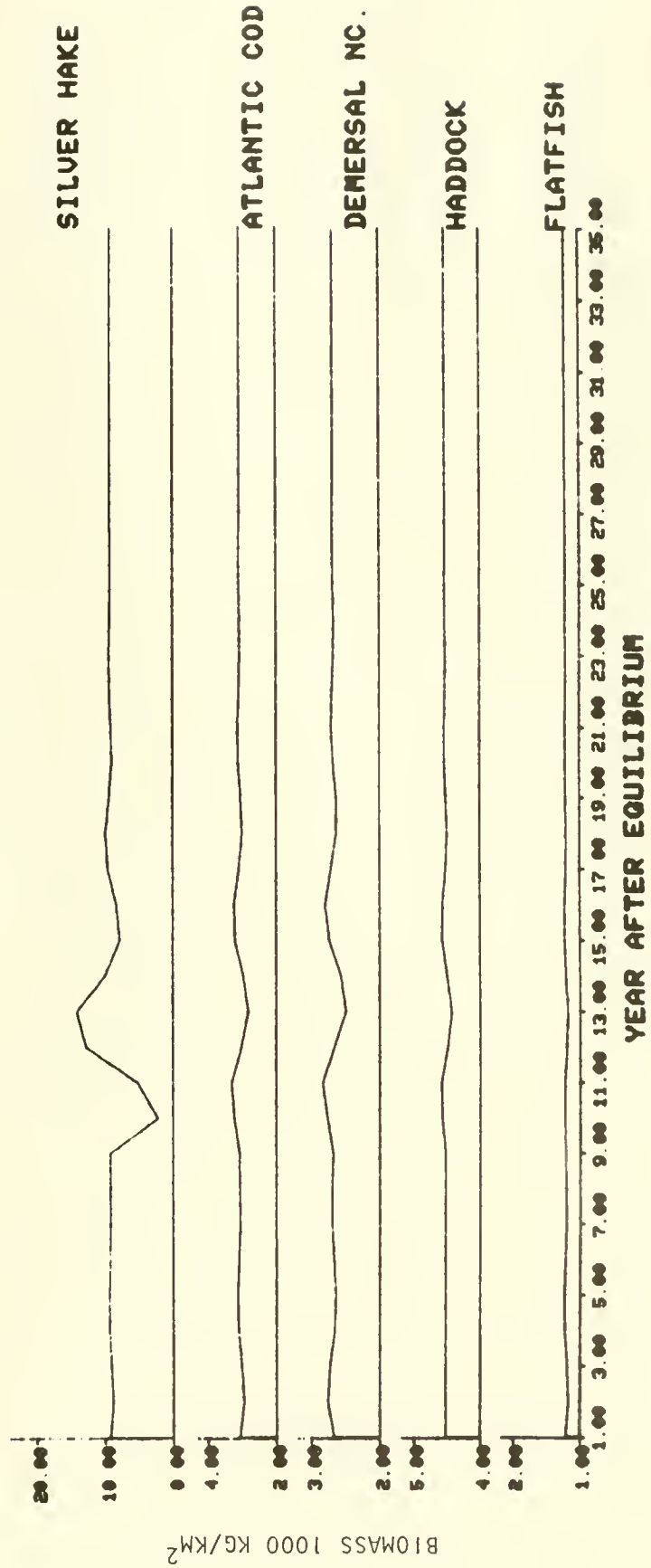


Figure 2. Annual mean biomasses of fish species groups and benthos after equilibrium, showing the effect of a 75% reduction in the biomass of the silver hake group at year 10.



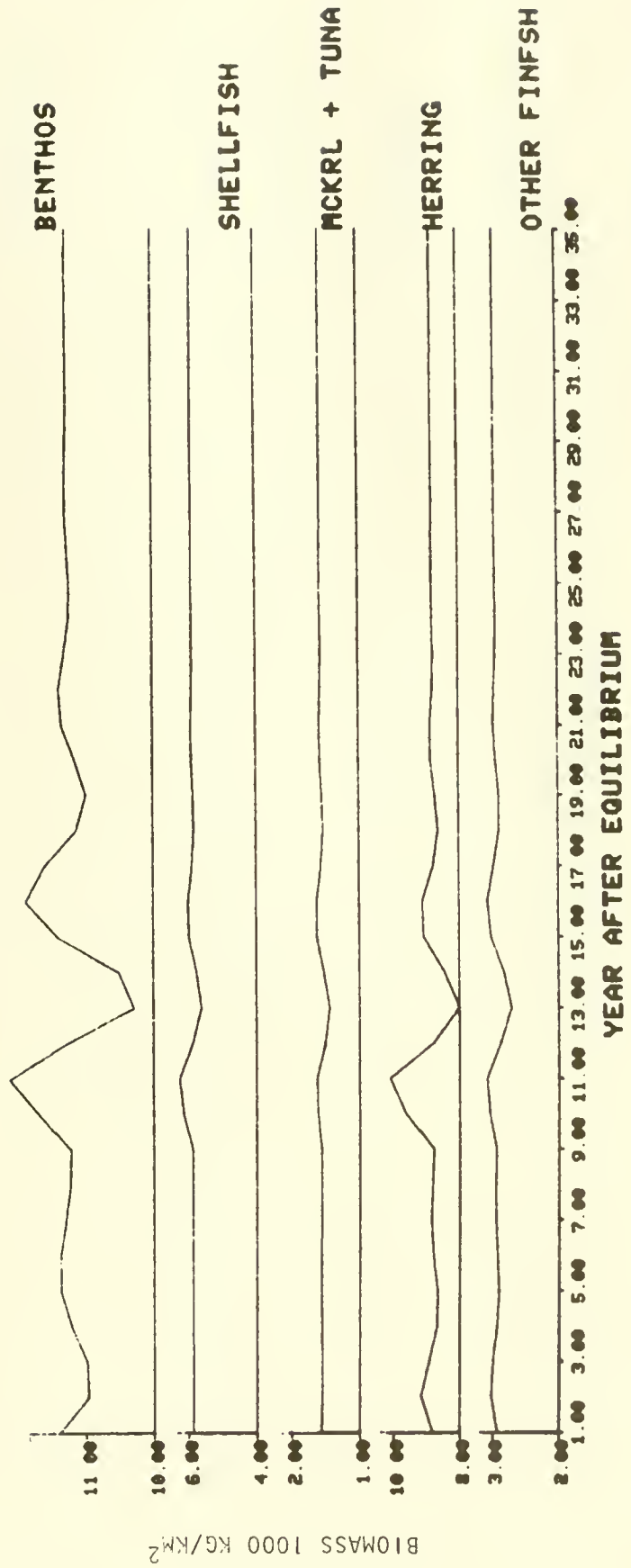


Figure 2. cont.



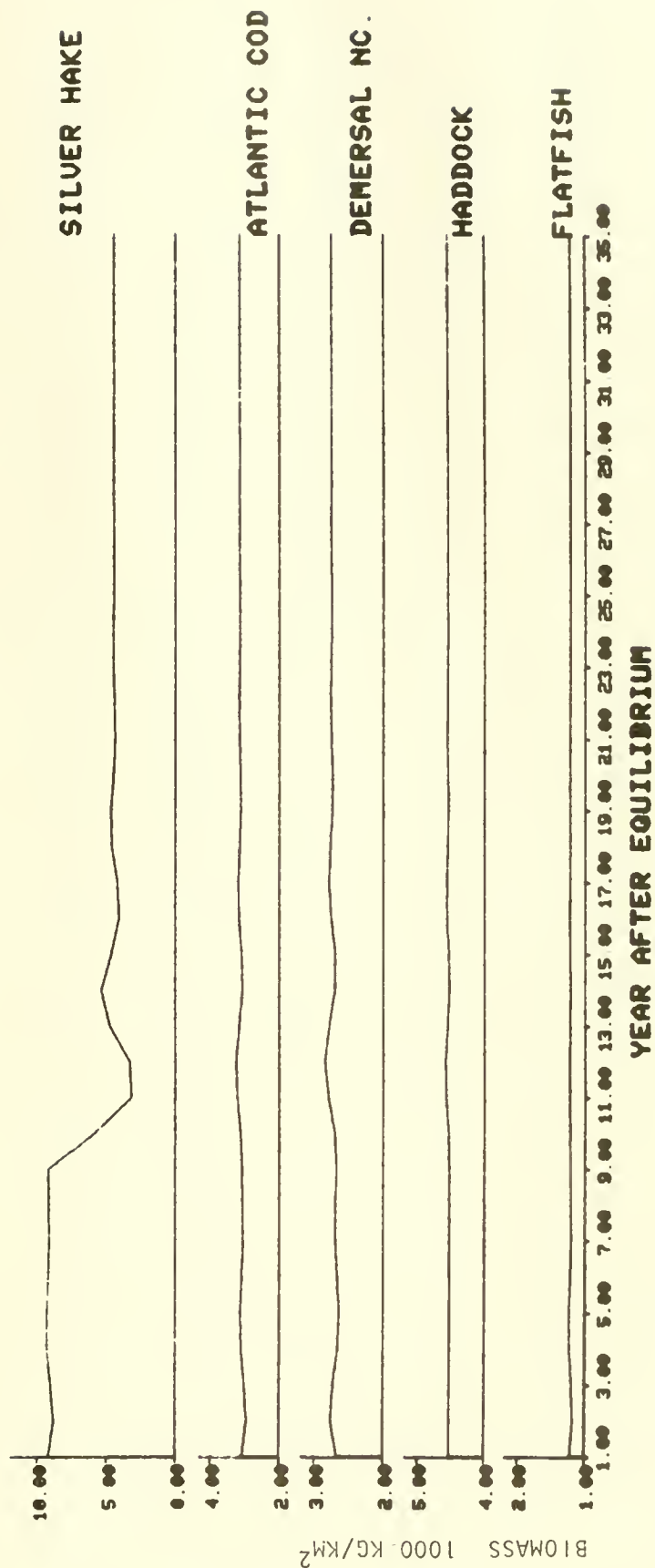


Figure 3. Annual mean biomasses of fish species groups and benthos after equilibrium, showing the effect of increasing the fishing pressure on the silver hake group fourfold at year 10.



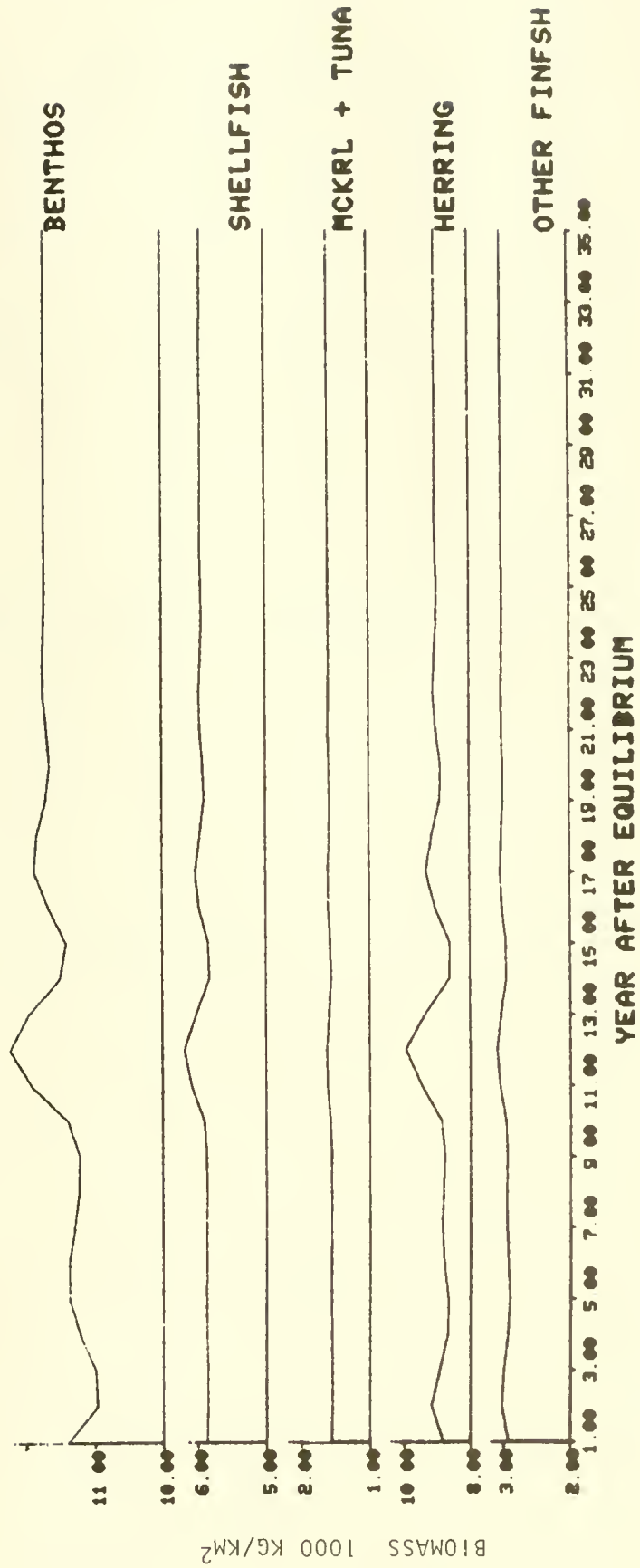


Figure 3. cont.





Table 1.--Preliminary output data from SKEBUB.

Species or group	Annual consumption of mean biomass (%)	Annual catch of mean biomass (%)	Mean daily food requirement as % of biomass	Percent of required food not obtained in month 3	Mean monthly growth coefficient
Flatfish	65	30	0.87	3.4	0.97
Haddock	50	18	0.78	3.4	0.75
Demersal NC.	62	2	0.80	7.6	0.81
Cod	74	30	1.05	6.9	1.04
Silver hake + pollock + redfish	74	30	1.03	10.3	1.06
Other finfish	79	2	1.03	6.7	0.99
Herring	72	14	1.03	8.2	1.05
Mackerel + tuna	76	14	1.11	11.9	0.99
Squids	190	-	0.52	14.6	-
Shellfish	51	14	0.71	3.6	0.78
Benthos	37	2	-	-	0.47



APPENDIX TABLES



Table 1.--Sample composition of biota for SKEBUB.

Group No.	Name	Species Composition
1.	Species 1	Any species under special consideration
2.	Flatfish	Yellowtail, winter flounder, etc.
3.	Haddock	Haddock
4.	Demersal nc.	Dogfish, skates, red hake, etc.
5.	Cod	Cod
6.	Semidemersal	Pollock, redfish, silver hake
7.	Other finfish	Argentines, sand lance, etc.
8.	Herring	Herring
9.	Pelagic	Mackerel, tuna
10.	Squids	Illex, loligo
11.	Shellfish	Commercial species, including lobsters
12.	Benthos	
13.	Zooplankton	
14.	Phytoplankton	

#### APEX PREDATORS

Birds (Fulmars, kittiwakes, storm petrels)

Mammals (Odontocete whales (fish feeders), fin and right whales, pilot whales, bottlenose dolphins)

Sharks

Man (Fishing)



TABLE 2.--Input biomasses and percent similarity in their diets.<sup>1/</sup>

Group No.	Species composition	Percent similarity	Input biomass (kg/km <sup>2</sup> )
1.	-	-	-
2.	Yellowtail Winter flounder	59%	600 <u>300</u> 900
3.	Haddock		4,500
4.	Dogfish Skates Red hake, etc	{ 7% 60%	{ 9% (500) (300) <u>1,100</u> 1,900
5.	Cod		1,900
6.	Pollock Redfish Silver hake	{ 69% 37%	{ 42% 300 100 <u>10,100</u> 10,500
7.	Other finfish		1,700
8.	Herring		19,300
9.	Mackerel Tuna		1,300 (200) <u>1,500</u>
10.	Illex Loligo		280 <u>400</u> 680
11.	Shellfish	6,300	
12.	Benthos	120,000	
13.	Zooplankton	45,000	
14.	Phytoplankton	60,000	

<sup>1/</sup> Data from Grosslein et al.





Table 3.--Sample inputs: initial biomasses, growth, mortality, and food coefficients.

Species group No.	V Initial biomass kg/km <sup>2</sup>	G Growth coeff.	SM Mortality coeff.	FK "Constant catch"	FRM Food maint.	FRG Food growth
1	-	-	-	-	-	-
2	900	0.075	0.005	0.025	0.5	1.32
3	4500	0.058	0.005	0.015	0.5	1.32
4	1900	0.065	0.008	0.002	0.5	1.32
5	1900	0.085	0.005	0.025	0.55	1.65
6	10500	0.090	0.005	0.025	0.52	1.65
7	1700	0.080	0.008	0.002	0.54	1.70
8	19300	0.085	0.005	0.012	0.55	1.60
9	1500	0.085	0.005	0.012	0.57	1.90
10	680	0.150	0.020	0.005	0.52	1.94
11	6300	0.060	0.010	0.012	0.43	1.25
12	120000	0.035	0.010	0.002	0.35	1.75
13	45000	-	-	-	-	-
14	60000	-	-	-	-	-



Table 4.--Monthly mean temperatures, acclimatization temperatures, and plankton parameters.

Month	Water temperature TM	Species Group number	Acclimatization temperature TA
1	7	1	
2	5.5	2	7.5
3	4.8	3	7.5
4	5.0	4	7.0
5	5.5	5	8.5
6	7.5	6	9.5
7	10.0	7	9.5
8	13.0	8	9.5
9	13.0	9	11.0
10	13.0	10	12.0
11	11.5	11	7.0
12	9.5	12	7.0
		13	-
		14	-

Phytoplankton:  $V(14) - 60 \text{ t/km}^2$  ZF-30 ZFKA-170

Zooplankton:  $V(13) - 45 \text{ t/km}^2$  ZZ-20 ZZKA-240



Table 5.--Parameters for simulation of monthly mean apex predator biomasses, and their food composition

Area:	53,000 km <sup>2</sup>				
Birds:	Mean 35 kg/km <sup>2</sup>	half magnitude of annual change	20	κ 220	18% BWD
Mammals:	Mean 200 kg/km <sup>2</sup>	half magnitude of annual change	120	κ 180	4.5% BWD
Sharks:	Mean 35 kg/km <sup>2</sup>	half magnitude of annual change	15	κ 180	2.2% BWD
Squids:	Mean 680 kg/km <sup>2</sup>	half magnitude of annual change	210	κ 180	(0.52 + 1.954 x G)

<u>Food item</u>	<u>Food composition</u>			
(Species group number)	Birds %	Mammals %	Sharks %	Squids %
1	-	-	-	-
2	2	2	3	2
3	2	3	2	6
4	5	8	15	4
5	5	8	12	3
6	7	8	12	8
7	13	12	15	8
8	10	4	10	12
9	4	5	10	6
10	10	18	12	7
11	4	5	2	2
12	2	6	2	1
13	36	21	5	41
14	-	-	-	-



Table 6.--Mean food composition of sample fish biota.

Species group number	% of species in food													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	0.5	3.0	1.0	0.5	3.2	4.0	4.2	0	1.0	1.0	55.0	26.6	-
3	-	0.5	3.0	1.0	0.5	3.2	4.0	4.2	0	1.0	1.0	55.0	26.6	-
4	-	2.0	5.0	7.0	4.0	3.2	9.0	4.2	4.0	2.0	4.0	40.0	15.6	-
5	-	4.5	7.0	5.0	3.5	6.2	4.0	8.0	1.0	1.0	5.0	37.0	17.8	-
6	-	0.5	10.0	5.0	4.0	6.5	6.0	12.0	1.0	3.0	4.0	20.0	28.0	-
7	-	1.0	4.0	3.0	3.0	6.0	2.0	4.0	1.0	1.0	2.0	22.0	51.0	-
8	-	1.0	2.0	1.0	1.0	3.6	2.0	4.2	1.0	0	2.0	1.0	81.2	-
9	-	1.5	5.0	3.0	2.0	6.5	6.0	8.0	6.0	3.0	2.0	1.0	56.0	-
10	-	2.0	6.0	4.0	3.0	8.0	8.0	12.0	6.0	7.0	2.0	1.0	41.0	-
11	-	1.0	1.0	1.0	1.0	1.0	2.0	3.0	1.0	1.0	1.0	50.0	37.0	-
12	-	1.0	1.0	1.0	1.0	1.0	2.0	3.0	1.0	1.0	1.0	36.0	31.0	20.0
13	-	-	-	-	-	-	-	-	-	-	-	-	30.0	70.0
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-







